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# SKELETAL STRENGTH OF ENCRUSTING CHEILOSTOME BRYOZOANS

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## Abstract

Encrusting cheilostome bryozoans structurally resemble aggregates of small boxes, with both frontal and vertical walls capable of resisting forces generated by water-borne debris or predators. Both the skeletal strength and design of the walls are important in determining the relative ability of the colony to resist damage. Two mechanical tests, puncture and compression, performed on nine species of tropical bryozoans reveal significant differences in skeletal strength both between species and between the outer and inner regions of colonies. Puncture stresses required to break through the frontal walls of zooids range from 0.8 to 291.0 $MNm^{-2}$ for edge zooids and from 1.1 to 457.4 $MNm^{-2}$ for inner zooids; compressive stresses required to damage the colony range from 4.4 to 16.9 $MNm^{-2}$ for edge regions and 6.5 to 27.2 $MNm^{-2}$ for inner regions. Ecological implications for these differences in skeletal strength are discussed with particular reference to resisting predation. From the mechanical test results, the material properties of shear strength (2.6–90.5 $MNm^{-2}$) and compressive strength (8.2–110.0 $MNm^{-2}$) are estimated for the frontal and vertical walls, respectively. Bryozoan wall material appears to be comparable in strength to such biological ceramics as coral, echinoid spine, bivalve shell, and vertebrate bone, but lower in strength than gastropod shell.

## Introduction

The Cheilostomata (with approximately 1000 genera) are the dominant group of bryozoans in Recent seas. Much of their evolutionary success has been explained in terms of the ways in which they have solved the problem of increasing calcification, and thereby the support and protection of soft tissues and feeding organs, without sacrificing the hydrostatic method of lophophore protrusion (Cheetham, 1971; Schopf, 1977). Cheilostomes vary widely in the extent of calcification. In the suborder Anasca, zooidal, basal, and vertical walls are usually calcified, while the frontal wall remains membranous to a greater or lesser extent (though overarching spines or an underlying cryptocyst may provide some protection). In contrast, bryozoans of the apparently polyphyletic suborder Ascophora exhibit varying modes of additional calcification of the frontal wall (Banta and Wass, 1979; reviewed in Hayward and Ryland, 1979), which can be further elaborated on by the development of thickened areas, tuberosities, and pores in various patterns.

Surprisingly, in view of the obvious importance of wall structure in the group, experimental studies of how well the skeleton strengthens or protects the zooids are lacking (Schopf, 1977). The only experimental work thus far relates primarily to the resistance of erect species to bending stress as induced by bottom currents or water-

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borne debris (Schopf *et al.*, 1980; Cheetham and Thomsen, 1981). Although the majority of cheilostome species are primarily or entirely encrusting, there has been no experimental work on skeletal strength of encrusting species, except for two species which were incidentally anlyzed to compare with erect species (Cheetham and Thomsen, 1981).

Zooids of encrusting cheilostomes resemble minature boxes with frontal, vertical, and basal walls surrounding the body cavity. In this study two different mechanical tests, puncture and compression, were performed in an attempt to elucidate the relative strengths of both frontal and vertical walls and their contribution to overall colony protection. Ordinarily, the basal walls of encrusting species are entirely adherent to a rigid substratum and thus not directly involved in strengthening the zooids. Pucture tests were also performed on two structures associated with frontal surfaces, ovicells and opercula. We report here the results of a study of zooid strength in nine species of encrusting cheilostomes, show that differences exist both between species and between inner and outer regions of colonies within a species, and provide some possible structural and ecological interpretations of these differences.

## Materials and Methods

Species studied were all from the cryptic coral reef habitat of Jamaica (Jackson and Winston, 1982; Winston and Jackson, 1984). Nine species—*Steginoporella* sp. nov., *Steginoporella magnilabris, Reptadeonella costulata, Reptadeonella bipartita, Trematooecia aviculifera, Parellisina latirostris, Parasmittina* sp., *Stylopoma spongites,* and *Drepanophora tuberculatum* (Fig. 1)—were collected at depths between 10 and 20 meters at two sites, Rio Bueno and Pear Tree Bottom, on the north coast of Jamaica. These species were chosen because they are the most abundant in these environments (Jackson, 1984).

Bryozoan colonies with their coral substrata were collected by diving, transported in sea water to the laboratory, and maintained there in running sea water until tested and measured.

### *Puncture test*

The first mechanical test performed was a "puncture" test, similar to a direct-shear or punching test (Faupel, 1964; Carter *et al.*, 1983), to measure the strength of frontal walls. A puncturing device (Fig. 2A) was constructed by sanding down the point of a straight pin, resulting in a flat blunt circular probe. The probe diameter was measured at 0.115 mm (area = 0.0139 mm$^2$). The surface area of the probe was measured periodically throughout the series of tests to ensure a constant area.

This puncturing probe was attached to a force platform which could be lowered vertically by a micromanipulator, pushing the probe perpendicularly down onto the surface of a colony, completely submerged in sea water. Viewing through a dissecting microscope allowed for precise placement of the probe on the frontal surface of a zooid, along the mid-line about one half of the way between the proximal wall and the operculum (as shown in Fig. 3F). The platform consisted of two steel beams (0.20 mm thick, 12.7 mm wide) held parallel, restricting bending to only one plane. A strain gauge (Bean, BAE-06-250BB-120TE, 120 ohm) was mounted on one steel beam. As the platform was lowered, the probe pushed against the frontal wall; this force was transmitted along the rod which connected the steel beams, bending both. The strain gauge measured the amount of deflection, or strain, which was recorded as a change in its electrical resistance, amplified by a bridge amplifier, and registered

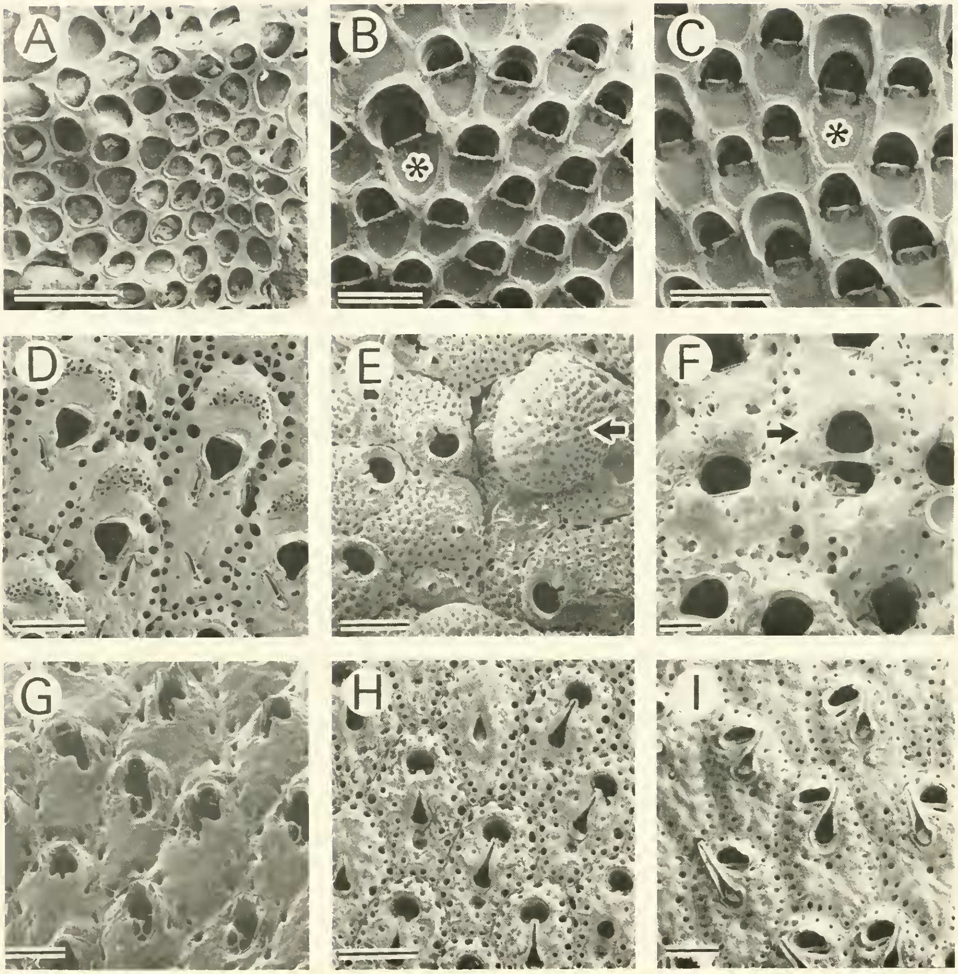


FIGURE 1. Cheilostome species tested showing appearance of frontal surfaces in skeletal (bleached) specimens. A. *Parellisina latirostris* (scale = 1 mm). B. *Steginoporella* sp. nov. (scale = 1 mm). C. *Steginoporella magnilabris* (scale = 1 mm). D. *Parasmittina* sp. (scale = 200 μm). E. *Stylopoma spongites* (scale = 200 μm). F. *Trematooecia aviculifera* (scale = 200 μm). G. *Drepanophora tuberculatum* (scale = 200 μm). H. *Reptadeonella bipartita* (scale = 400 μm). I. *Reptadeonella costulata* (scale = 200 μm). Arrows point to ovicells of *Stylopoma* and *Trematooecia*. Asterisks mark B-zooids in *Steginoporella*.

on a dual channel chart recorder. Once the gauge output is calibrated, this deformation is an indirect measure of the force placed on the colony by the probe.

By inverting the force platform and adding known weights to the probe, the output of the gauge could be calibrated to the nearest $1 \times 10^{-5}$ N. Calibrations were repeated before and after testing each species. In all the tests, the force platform was lowered at approximately the same rate to ensure nearly uniform loading rates.

The core to a linear variable differential transformer (LVDT Schaevitz 24v, Type 100-HR) was placed along the length of the rod connecting the steel beams to the probe. This transformer recorded the "displacement" (to the nearest $1 \times 10^{-5}$ mm) of the probe, *i.e.*, the distance the probe traveled as it was forced onto the skeleton,

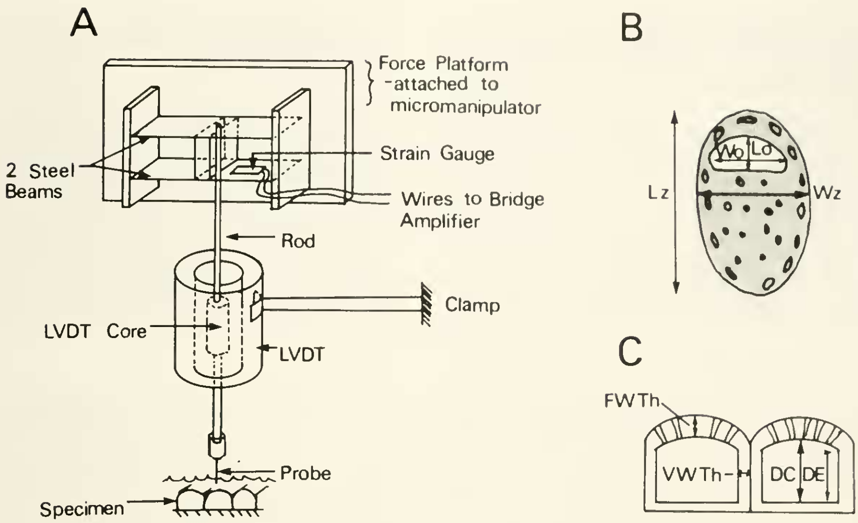


FIGURE 2. A. Diagram of apparatus used to measure skeletal strength of encrusting cheilostome bryozoans. B. Diagram of cheilostome zooid showing standard measurements made on frontal surfaces of zooids. Lz = zooid length. Wz = zooid width. Wo = orifice width. Lo = orifice length. C. Transverse section through two cheilostome zooids, showing other measurements taken. FWTh = frontal wall thickness. VWTh = vertical wall thickness. DC = depth of zooid cavity (center). DE = depth of zooid cavity (edge).

measuring the deformation of the frontal wall before breaking. Displacement registered on the second channel of the chart recorder, resulting in simultaneous reading of both the force applied to and the deformation of the surface.

The forces required to puncture zooecia in the middle and along the growing edge of a colony were recorded for eight species. In addition, both A and B zooids from the inner region of *Steginoporella* sp. nov. were tested. Puncture forces were also recorded for opercula (*e.g.*, Fig. 3A) and ovicells (*e.g.*, Fig. 1E, F) in several species.

*Compression test*

The same procedures and equipment as in the puncture test were used but with a different probe. A flat end of a drill bit, 0.800 mm in diameter, served as the probe, covering an area 0.503 $mm^2$. Because zooid size varied between species, the probe spanned between 1 and 5 zooids. Whereas in the puncture test the probe punctured only the frontal wall, in the compression test the vertical walls were primarily involved in resisting the compressive forces of the larger probe.

In the compression tests only growing edge zooids and inner zooids were used. Both regions were tested in six species, inner zooids only in three more.

*Morphometrics*

After each colony was tested it was measured (live) under the dissecting microscope. For each specimen measurements to the nearest .009 mm were made of length and width of zooids and opercula (Fig. 2B) from both inner and edge regions, and length and width of ovicells if present. Colonies were then broken and examined in side

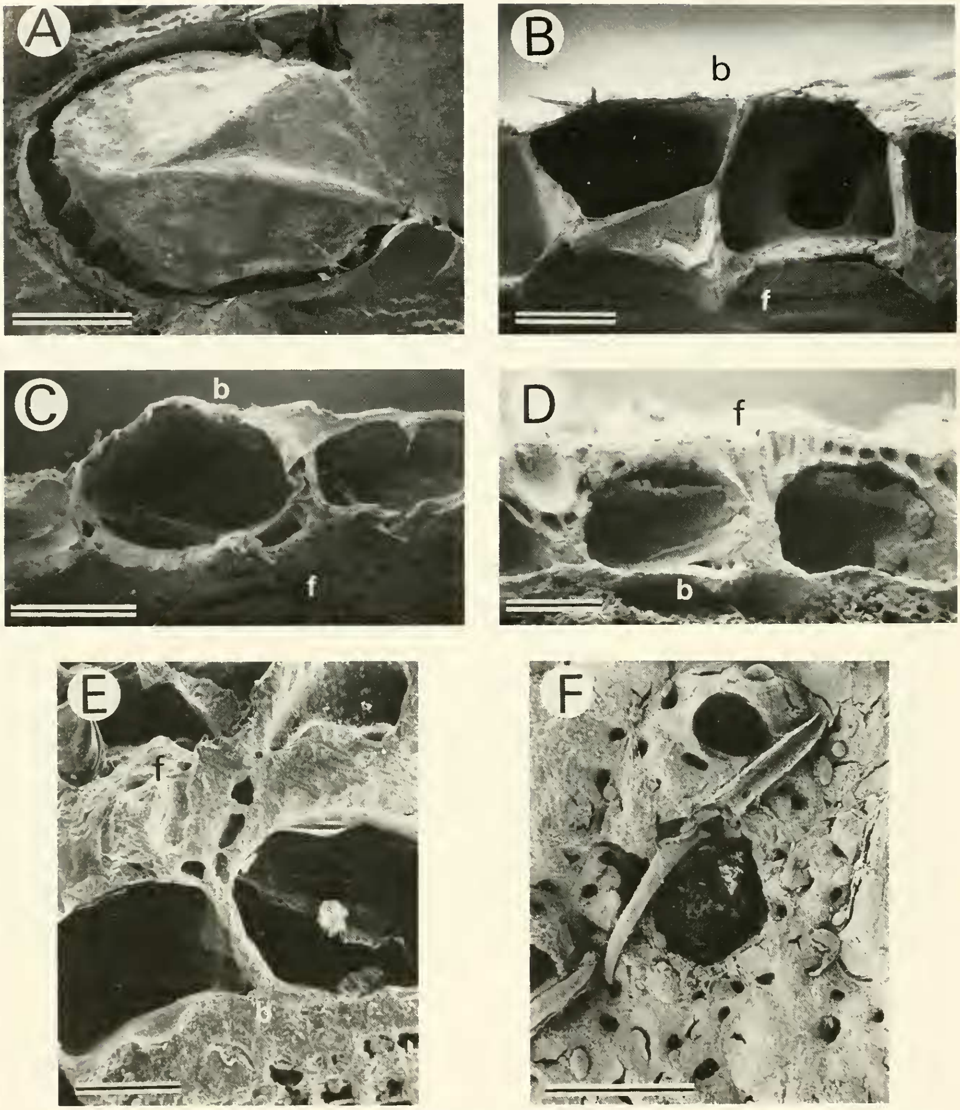


FIGURE 3. All scanning electron micrographs of dried specimens. A. Operculum of B-zooid of *Steginoporella magnilabris* (scale = 100 $\mu$m). B. Transverse view of *Steginoporella* sp. nov. zooids (scale = 300 $\mu$m). C. Transverse view of *Stylopoma* zooids (scale = 200 $\mu$m). D. Transverse view of *Reptadeonella costulata* zooids showing thick vertical and frontal walls (scale = 200 $\mu$m). E. Transverse view of *Trematooecia* zooids showing extremely thick frontal walls, but thin vertical walls (scale = 200 $\mu$m). F. A-zooid of *Reptadeonella costulata* showing effect of puncture (scale = 200 $\mu$m). F = Frontal wall. B = Basal wall.

view to determine frontal wall thickness, vertical wall thickness, and zooid depths at center and edges (Fig. 2C, Fig. 3B–E). Photographs of frontal surfaces of zooids were used to determine both the surface area and perimeter of individual zooids. The length of lateral and transverse walls were measured separately in order to determine the total vertical wall area supporting the zooids under the probe.

*Naturally occurring skeletal damage*

Additional colonies from Rio Bueno were specially collected, cushioned in plastic bags and very carefully transported to the laboratory to be examined for naturally occurring injuries. For each species tested (except *Parellisina latirostris*) several colonies were examined and types of damage to zooids and larger colony areas noted.

## Results

*Puncture tests*

*Zooids.* All notations and equations of derived measurements are listed in Appendix 1. Results of the puncture tests of both edge and inner zooids are presented in Appendix 2. Forces (F) applied to zooids were divided by the area of the probe ($A_p$, $1.039 \times 10^{-8}$ $m^2$) to give the applied stress or force per unit area ($F/A_p$). Values given are the ultimate stress applied before breakage occurred, representing the "puncture strength." The breaking force was also divided by the circumference of the probe ($3.616 \times 10^{-4}$ m) times the frontal wall thickness ($T_f$) of each species to determine the force per unit area of material in shear ($F/2\pi RT_f$), the "breaking shear stress," which is a material property.

Scheffé's multiple comparison of means procedure (Scheffé, 1959) was used to evaluate significant differences in both puncture strength and shear strength values between species for each edge and inner region (Tables I, II) and within species between the edge and inner regions (Table III).

Table I

*Comparison of puncture strength between species for inner and edge zooids*

| Region/species | Stress ($MNm^{-2}$) |
|---|---|
| A. Inner zooids | |
| *Parellisina* | 1.1 |
| *Steginoporella magnilabris* | 7.0 |
| *Steginoporella* sp. nov. A-zooid | 8.0 |
| *Steginoporella* sp. nov. B-zooid | 11.8 |
| *Reptadeonella costulata* | 159.6 |
| *Stylopoma* | 221.0 |
| *Drepanophora* | 286.0 |
| *Reptadeonella bipartita* | 327.3 |
| *Trematooecia* | 457.4 |
| B. Edge zooids | |
| *Parellisina* | 0.8 |
| *Steginoporella megnilabris* | 2.2 |
| *Steginoporella* sp. nov. A-zooid | 5.0 |
| *Stylopoma* | 33.7 |
| *Reptadeonella costulata* | 67.7 |
| *Drepanophora* | 83.9 |
| *Reptadeonella bipartita* | 126.8 |
| *Trematooecia* | 291.0 |

Values are mean puncture strengths. Refer to Appendix 2 for sample sizes. There are no statistically significant differences among species within the brackets; all other differences are significant, Scheffé test, $\alpha = 0.05$.

TABLE II

*Comparison of shear strength between species for inner and edge zooids*

| Region/species | Shear stress ($MNm^{-2}$) |
|---|---|
| A. Inner zooids | |
| *Parellisina* | 4.8 |
| *Steginoporella magnilabris* | 7.5 |
| *Steginoporella* sp. nov. A-zooid | 9.2 |
| *Steginoporella* sp. nov. B-zooid | 10.6 |
| *Reptadeonella costulata* | 32.8 |
| *Drepanophora* | 75.4 |
| *Stylopoma* | 87.1 |
| *Trematooecia* | 89.5 |
| *Reptadeonella bipartita* | 90.5 |
| B. Edge zooids | |
| *Parellisina* | 2.6 |
| *Steginoporella magnilabris* | 2.9 |
| *Steginoporella* sp. nov. A-zooid | 6.5 |
| *Reptadeonella costulata* | 17.7 |
| *Stylopoma* | 17.6 |
| *Drepanophora* | 22.1 |
| *Reptadeonella* | 44.5 |
| *Trematooecia* | 83.7 |

Values are mean shear stresses applied for breakage, *i.e.*, shear strengths. Refer to Appendix 2 for sample sizes. There are no statistically significant differences among species within the brackets; all other differences are significant, Scheffé test, $\alpha = 0.05$.

*Opercula.* Breaking strengths of opercula were recorded in two ways (Appendix 2). In most cases, the opercular hinge broke as relatively low forces were applied; with increasing loads the probe either broke through the frontal wall of the operculum, or in cases where the probe was larger than the lid, shattered the orifice. A Scheffé test ($\alpha = 0.05$) was used to determine differences in the hinge-breaking stress between species and between A and B zooids of the same species, where applicable.

Opercula of *Steginoporella* sp. nov. A and B zooids were the strongest (4.56 and 6.04 $MNm^{-2}$), were not different from each other, but were significantly different

TABLE III

*Within-species differences in puncture strength and shear strength between edge and inner regions*

| Species | Puncture strength | Shear strength |
|---|---|---|
| *Drepanophora* | * | * |
| *Parellisina* | ns | ns |
| *Reptadeonella bipartita* | * | * |
| *Reptadeonella costulata* | * | * |
| *Steginoporella magnilabris* | * | * |
| *Steginoporella* sp. nov. A-zooid | ns | ns |
| *Stylopoma* | * | * |
| *Trematooecia* | ns | ns |

* Significant difference between inner and edge zooids in strength, Scheffé test, $\alpha = 0.05$. ns, not significant.

(Scheffé test, $\alpha = 0.05$) from *Steginoporella magnilabris* (1.59 $MNm^{-2}$) and *Stylopoma* (2.49 $MNm^{-2}$). *Trematooecia* (2.73 $MNm^{-2}$) showed no significant difference from the other species.

*Ovicells.* Ovicells from four bryozoan species were tested for puncture strengths (Appendix 2). *Drepanophora* (94.59 $MNm^{-2}$) and *Stylopoma* (70.27 $MNm^{-2}$) were significantly different (Scheffé test, $\alpha = 0.05$) from *Trematooecia* (22.11 $MNm^{-2}$). *Parellisina* (52.82 $MNm^{-2}$) was not different from the others.

*Compression tests*

The results from the compression tests are listed in Appendix 3. As in the puncture test, breaking forces were converted to force per unit area probe ($A_p = 5.026 \times 10^{-7}$ $m^2$), or "breaking stress." From the morphometrics a mean value of the total vertical wall area ($A_v$) under the probe was calculated for each region. This vertical wall area is an estimate of the wall area resisting the compressive force of the probe. Using the mean compressive force for each region, a mean value of force per total vertical wall area ($F/A_v$) was derived (Appendix 3).

Differences in compressive breaking stress between species were tested for inner and edge regions by a Scheffé test (Table IV). Differences within species between edge and inner regions or between inner A and B zooids are given in Table V.

During the compression tests, observations were made on the nature of breakage for each species. Colonies of *Parasmittina* and *Parellisina* shattered under compression; large cracks radiated outward from the area under stress. *Trematooecia* shattered downward rather than laterally, pulverizing the underlying zooids but not the neigh-

TABLE IV

*Comparison of compressive strength between species for inner and edge regions*

| Region/species | Compressive strength ($MNm^{-2}$) |
|---|---|
| A. Inner region | |
| *Parellisina* | 6.5 |
| *Steginoporella magnilabris* A-zooid | 11.3 |
| *Stylopoma* | 12.9 |
| *Trematooecia* | 13.3 |
| *Steginoporella magnilabris* B-zooid | 14.7 |
| *Steginoporella* sp. nov. A-zooid | 14.9 |
| *Parasmittina* | 15.8 |
| *Reptadeonella bipartita* | 23.8 |
| *Reptadeonella costulata* | 26.8 |
| *Drepanophora* | 27.2 |
| B. Edge region | |
| *Steginoporella* sp. nov. A-zooid | 4.4 |
| *Stylopoma* | 6.3 |
| *Trematooecia* | 7.0 |
| *Reptadeonella bipartita* | 12.6 |
| *Reptadeonella costulata* | 14.3 |
| *Drepanophora* | 16.9 |

Values are mean compressive strengths. Refer to Appendix 3 for sample sizes. There are no statistically significant differences among species wihtin the brackets; all other differences are significant, Scheffé test, $\alpha = 0.05$.

TABLE V

*Within species differences in compressive strength between edge and inner regions or between A- and B-zooids*

| Species | Regions | Compressive strength |
|---|---|---|
| *Drepanophora* | Edge *vs.* Inner | * |
| *Reptadeonella bipartita* | Edge *vs.* Inner | ns |
| *Reptadeonella costulata* | Edge *vs.* Inner | * |
| *Steginoporella magnilabris* | A- *vs.* B-zooids | ns |
| *Steginoporella* sp. nov. | Edge *vs.* Inner | * |
| *Stylopoma* | Edge *vs.* Inner | * |
| *Trematooecia* | Edge *vs.* Inner | * |

* Significant difference between regions in strength, Scheffé test, $\alpha = 0.05$. ns, not significant.

boring ones. These three species had the smallest displacement, or downward movement of the probe, before breakage (Appendix 3). *Parasmittina* and *Parellisina* can be characterized as "brittle" material; during compression the material undergoes little deformation until the breaking stress is reached and then shatters explosively as energy is released. Propogating cracks resulted in more extensive damage to the colony. Shattering in the "rigid" *Trematooecia,* with its heavily calcified frontal walls, occurred when the applied load buckled the thinner vertical walls (Fig. 3E). In the other six species damage was localized and restricted to the area under the probe or immediately adjacent; higher displacements recorded in this group resulted from the vertical walls crushing rather than buckling.

## *Morphometrics*

Direct measurements on zooecial characteristics are presented in Appendix 4 (for all species except *Parasmittina* sp.). These measurements were then used to calculate derived measurements (refer to Appendix 1): number of zooids per probe area ($Z_a$), total vertical wall area per probe area ($A_v$), and curvature of the frontal wall (C). An estimate of the frontal wall curvature (C) was derived by subtracting the depth of the zooid cavity edge (DE) from the depth of the zooid cavity at the center (DC), and dividing by the zooid width ($W_z$). Correlations between both direct and derived measurements were run against compressive breaking force (Table VI). For the puncture test results, the mean displacement of the probe for each species was negatively

TABLE VI

*Correlations of structural parameters with compressive breaking force*

| Parameter | *r* | Prob > *r* | # Obs. | Region |
|---|---|---|---|---|
| # Zooids/probe area, ($Z_a$) | 0.399 | 0.286 | 9 | inner |
| Vertical wall thickness, ($T_v$) | 0.673 | 0.067 | 9 | inner |
| Frontal wall thickness, ($T_f$) | 0.678 | 0.065 | 8 | inner |
| Total vertical wall area, ($A_v$) | 0.833 | 0.010* | 8 | inner |
| $A_v$ x Puncture shear strength | 0.853 | 0.008** | 8 | inner |
| | 0.960 | 0.002** | 6 | edge |

* Denotes $P < 0.05$. ** indicates $P < 0.01$. # Obs. refers to the number of species used in the correlation.

correlated with increasing curvature of the frontal wall ($r = -0.69$, $P = 0.039$) and with the mean shear strength ($r = -0.81$, $P = 0.007$).

### *Naturally occurring skeletal damage*

No new injuries could be detected in the one colony of *Parellisina latirostris* obtained except where zooids had been punctured.

The species showing the greatest amount of frontal wall injury was *Stylopoma spongites*. Many of these injuries consisted of fractures extending over the surfaces of several zooids, or large irregularly shaped patches on the frontal wall of a single zooid.

In colonies of *Reptadeonella costulata* zooids and buds around the margin showed signs of pruning by grazers. The most common injury, however, consisted of abrasion of the outer cuticle and epithelium from part or all of the frontal surface. One zooid had a puncture through the avicularium-spiramen area in the center of the frontal wall. Other colonies were attacked or colonized from beneath by boring sponges and spionid-like polychaetes. Injuries to *Reptadeonella bipartita* followed a similar pattern with some injuries caused from below by the activities of sponges and polychaetes and some by frontal abrasion.

In the most common type of injury to a single zooid of *Steginoporella* sp. nov. the operculum was missing but the skeleton was undamaged; the tissue was gone and there was often a copepod in the zooid interior. In addition to single zooid injuries, "bite-marks" covering groups of zooids (several $mm^2$ in area) were also noted; there were even larger grazed areas present in old areas of colonies and along the growing margin.

Colony margins of *Drepanophora tuberculatum* showed signs of pruning by grazers, while zooids in the inner regions appeared undamaged except for abrasion of the frontal surface. No injuries were observed on the colonies of *Trematooecia aviculifera* examined, though old injuries may have been obscured by frontal budding.

## Discussion

Studies of bryozoan ecology have shown that certain types of predators are common to most ecosystems: single zooid predators—some nudibranchs and pycnogonids—and grazers—urchins, nudibranchs, fish (Ryland, 1976; Seed, 1976; Nybakken and McDonald, 1981; Todd, 1981; Yoshioka, 1982). Another factor in bryozoan ecology is the potential for physical abrasion due to water-transported particles or rubble. Both inner and outer regions of colonies were tested for skeletal strength because it seemed obvious that zooids of the growing edge, in which calcification or development could still be incomplete, might be more susceptible to damage.

Damage to colonies in the field may occur under a variety of loading situations including shear, compression, abrasion, and complex combinations of these. In order to analyze the *relative* strength of bryozoans, we have made several simplifying assumptions: (1) That zooids can be modeled as little boxes, with forces being resisted primarily by the frontal and vertical walls. This assumption neglects the role that additional struts may play in shoring up the skeleton. (2) That the pure puncture or compression tests performed model the action of either impacting debris or a predator. Nudibranch radulas tend to exert a rasping, abrading, or shear action, while grazing, like that of urchins and fish, involve both shear and compression. We assume here that "rasping" resistance is correlated with "shear" strength and that "grazing" resistance is correlated with "compressive" strength, and thus our tests give a relative measure of "resistance to predation." It is know that the "hardness," as measured by the Vickers hardness number, of a crystalline material is not only indicative of the material's resistance to abrasion, but also is correlated with the shear strength and tensile strength of the material (refer to Vincent, 1982). However, it must be noted that in rasping and grazing the exact geometry of the cutting edges employed by predators significantly affects their effectiveness. Therefore, in order to study the ability of a group of organisms to resist one particular predator, it would be necessary to replicate the exact morphology of the mandibles or radulas and their cutting motion.

### *Puncture tests*

*Puncture strength.* The puncture stress is the force per area that would be needed by the potential predator to break into the bryozoan zooid through the frontal wall. Although there are obviously many different factors involved in preying on bryozoans, puncture strength may be one determinant. Most nudibranchs that feed on bryozoans seem to prefer those with mostly membranous frontal walls, but at least some species attack well calcified ascophorans (Ryland, 1976). There is some evidence that nudibranchs which do feed on well-calcified forms may be more specialized in diet than those that prey on membranous forms, perhaps possessing radulas that can mechanically produce the forces necessary to puncture calcified walls (Nybakken and McDonald, 1981).

*Parellisina,* the only species with a membranous frontal wall, was by far the weakest with respect to puncture strength. Next strongest were both A and B zooids of *Steginoporella* sp. nov. and *Steginoporella magnilabris.* None of these species showed evidence of puncture wounds in the field, but in all of them soft tissue was apparently removed from the frontal surface by abrasion without evidence of puncture. *Stylopoma, Reptadeonella costulata,* and *Drepanophora* were intermediate with regards to puncture strength. Two of these species, *Reptadeonella costulata* and *Stylopoma,* showed evidence of pucture damage to individual zooids in specimens surveyed. *Trematooecia* and *Reptadeonella bipartita,* both of which showed no such damage, were the strongest overall.

In five out of eight species edge zone zooids were significantly weaker (half of them were only half as strong) than inner zooids, suggesting that some species may have regions more vulnerable to damage. This comparative weakness may be due to the rate and nature of the mineralization process during development.

*Puncture shear strength.* Puncture shear strength ($F/2\pi RT_f$) is a parameter of the frontal wall material, independent of thickness, and thus can be used to compare the material properties of the species tested. Differences in shear strength can be due to variations in ultrastructure and in both the mineral and organic composition. Closely related species such as *Steginoporella magnilabris* and both A and B zooids of *Steginoporella* sp. nov. had similar shear strengths. The two *Reptadeonella* species, on the other hand, showed about a three-fold difference in strength. As *Reptadeonella* was instituted as a convenience genus for all encrusting adenoid species (Harmer, 1957), this difference may signify that the two species are not congeneric, but more distantly related, a possibility supported by some other morphological features (Winston, unpub. data).

With regard to edge *versus* inner zooids the pucture shear strength showed exactly the same trends as puncture strength. Thus, the differences in puncture strength seen between the two regions are not attributable to differences in the thickness of the frontal wall (which varies with age), but indicate a difference in the ultrastructure itself, perhaps due to the development of the mineral-organic matrix. This regional difference in material strength in the encrusting bryozoan species studied here contrasts with work on erect species by Cheetham and Thomsen (1981); in the arborescent bryozoans they studied, there is no difference in material bending strength between thinly and thickly calcified parts of the colony.

In the puncture tests, there was a negative correlation between probe displacement and both shear strength and frontal wall curvature. It appears that a higher shear strength and greater curvature results in a more rigid zooecium, undergoing less deformation for a given force. The work (which equals force times displacement) required for puncture is higher in these more rigid forms.

*Opercula strength.* The force required to break opercular hinges is relatively low; it is not known how much force would be required to remove the operculum entirely (which may be the important parameter to some predators). Several nudibranchs known to attack the opercular area all appear to remove the operculum by sucking it open. This mode of feeding is more common on prey with membranous frontal walls, although a Ghanaian species of *Corambe* (Mollusca) does feed on a *Trematooecia* species in this manner (Ryland, 1976).

Although in two species the orifice shattered at forces lower than those required to break the frontal walls, injuries surveyed showed no tendency for predators to attack the orifices. There may be some other reasons why predators would be unlikely to attack opercula. Nudibranchs feed by puncturing with the radula, forming a seal around the puncture with the mouth, and then sucking out the zooid contents. Nudibranchs may not be able to form a good seal around puncture holes in the operculum area, perhaps due to shattering during breakage.

*Ovicell strength.* Ovicells in three of the four species tested were significantly lower in strength than the frontal walls. These three species, *Stylopoma, Drepanophora,* and *Trematooecia* have among the most robust inner zooids. Interestingly the species with the weakest frontal wall, *Parellisina* (1.14 $MNm^{-2}$) had a much stronger ovicell (52.8 $MNm^{-2}$), perhaps to prevent damage to, or discourage predation on, the enclosed egg.

### *Compression tests*

Compressive strength, the force per probe area, is a measure of the force required to induce damage to several zooids in a colony. In this test the vertical walls supply most of the resistive force, rather than the frontal walls which supply most of the resistive force in puncture tests. Colony injury could be induced by predators biting or grazing an area of zooids as well as by rubble striking the colony.

The two *Reptadeonella* species and *Drepanophora* were the species with the highest compressive strengths. The survey showed that they were subjected to a large amount of abrasion in which the surface layer of tissue was removed, but the underlying skeleton remained intact, and had colony margins which were heavily grazed. Previous studies at Rio Bueno (Winston and Jackson, 1984) had shown that these three species were the ones most able to survive intense damselfish grazing at one panel site. The other species which also had a high survival rate at this site was *Parasmittina* sp., the next strongest species according to the compression test (although significantly below the top three). All other species showed lower, relatively similar compressive strengths, with *Parellisina* being the weakest.

Thus, it appears that the susceptibility or resistance of a species to damage induced by physical factors or particular predators may be explained, as well as predicted, by its skeletal strength. The edge zones of the three strongest species were as strong as the inner zooids of the other species; this suggests that skeletons of similar or weaker strength, which include the entire colony of the weaker species, would be susceptible to predation. Distributions, as well as abundances, of bryozoans may be heavily influenced by their skeletal strengths.

*Correlation with colony morphology.* Compression tests were designed to measure the relative contribution of vertical walls to resisting force applied to the colony. The thickness of the frontal wall was not significantly correlated with compressive strength (Table VI), suggesting that the vertical walls contribute more than the frontal wall under this kind of test. Compressive strength was also not correlated with the number of zooids per probe area, indicating that having numerous small zooids does not necessarily lead to increased strength. However, total vertical wall area ($A_v$) was significantly correlated ($r = 0.83$, $P = 0.01$) with compressive strength. For example, of the three strongest species, one, *Drepanophora,* had the smallest zooids of the species tested and the others had intermediate sized zooids.

As a first order approximation it seemed reasonable to assume that material properties of both frontal and vertical walls would be approximately of the same value, although there are often ultrastructural differences between the two areas. We derived a new parameter with units of force using puncture shear stress times the total vertical wall area. This parameter was highly correlated with compressive strength ($r = 0.85$, $P = 0.008$ inner region; $r = 0.96$, $P = 0.002$ edge region), indicating that the differences in compressive strength can be explained by considering both the vertical wall area resisting that force and some measure of the wall's material strength.

*Comparative material strength*

In this study we were able to measure one material property, that of shear strength, and to derive an estimate of another, compressive strength, by estimating the vertical wall area under stress. The shear strength and compressive strength of various other natural and man-made materials are listed in Table VII as a comparison of the range of values these material properties assume.

Most of the bryozoan wall material studied can be classified as "biological ceramics," substances composed of a crystalline material, such as a calcium salt, with an organic matrix. Both the ratio of organic to mineral content and the nature of the crystalline structure may influence the material's strength. Limestone, a natural ceramic, and concrete, a man-made ceramic, lack any organic matrix and exhibit strengths below that of some bryozoans (Table VII). The compressive strength of concrete can be increased dramatically by the inclusion of a small percent of the polymer polymethylmethacrylate. This polymer is thought to act similarly to an organic matrix by bonding the constituents more tightly, thereby decreasing stress concentrations (refer to Vincent, 1982).

Although the presence of a small amount of organic material may strengthen a ceramic, strength may decrease if the percent of organics becomes too high. One of the more important determinants of tensile strength in vertebrate bone is the percent of mineral (Currey, 1969); the higher the mineral content, the stronger the material.

TABLE VII

*Comparison of shear strength and compressive strength of bryozoans with other natural and man-made materials*

| Material | Shear strength ($MNm^{-2}$) | Compressive strength ($MNm^{-2}$) |
|---|---|---|
| Bryozoans | 2.9–90.5 | 8.2–110.0[1] |
| Cedar[2] | 6.1 | 35.9 |
| Coral skeleton[3] | — | 12–81 |
| Gastropod shell[4] | — | 196–353 |
| Bivalve shell[4] | — | 82–419 |
| Echinoid spine[5] | — | 48–72 |
| Horse femur[6] | 97 | 142 |
| Concrete[7] | — | 6.9–62.1 |
| Limestone[7] | 6.2–15.9 | 17.9–144.8 |
| Porcelain[7] | — | 689.6 |

[1] Per vertical wall area, not probe area.
[2] Eshbach and Sounders, 1975.
[3] Chamberlain, 1978.
[4] Currey, 1976.
[5] Weber *et al.* 1969.
[6] Adapated from Yamada, 1970.
[7] Mantell, 1958.

Bryozoan wall compressive strength shows a range of values comparable to other biological ceramics—such as coral, bivalve shell, echinoid spine, and vertebrate bone—but appears to be lower than gastropod shell (Table VII). Different structural types of shell material—*e.g.*, nacre, crossed-lamellar, foliated—in molluscs have different compressive and tensile strengths (Currey, 1976). In contrast, Cheetham and Thomsen (1981) in their study of aborescent bryozoan skeletons found that the modulus of rupture, a property used to compare strength in bending, was not related to either skeletal composition (calcite *vs.* aragonite) or microstructure (lamellar *vs.* spherulitic). In this study we did not examine the microstructure of the walls tested, and thus can not draw any inferences between ultrastructure and strength. However, future research might examine the possible relationship between the percent of organics and strength in bryozoan skeletons. In this study the only species with an uncalcified, membranous frontal wall had an extremely low value for wall shear strength.

In summary this study has found that species-specific differences exist in the stresses required to either puncture individual zooids or to crush parts of a colony. These differences appear to be due to both zooid architecture and material properties of the walls. Colony compressive strength may be a useful indicator of "resistance to predation" from grazers, and may be a determinant of species abundances and distributions in areas subjected to heavy predation.

Two measurements of material properties—shear strength of frontal walls and compressive strength of vertical walls—also show species-specific differences, as well as significant within-colony differences. These material properties span a wide range of values, and may be indicative of ultrastructural differences in the organic-mineral matrix.

Bryozoan wall material appears to be stronger than some natural ceramics, comparable in strength to such biological ceramics as coral, echinoid spine, bivalve shell, and vertebrate bone, but lower in strength than gastropod shell.

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## APPENDIX I

*Notation and derived measurements*

| | |
|---|---|
| A | Area |
| $A_p$ | Cross-sectional area of probe |
| $A_v$ | Total vertical wall area per probe area |
| $A_z$ | Zooid area |
| C | Frontal wall curvature, $(DC - DE)/W_z$ |
| DC | Depth of zooid cavity (center) |
| DE | Depth of zooid cavity (edge) |
| F | Force |
| $L_l$ | Length of lateral wall |
| $L_o$ | Orifice length |
| $L_t$ | Length of transverse wall |
| $L_z$ | Zooid length |
| N | Newton |
| $P_z$ | Zooid perimeter (length of vertical walls) |
| R | Radius |
| | Stress, $F/A_p$ |
| | Shear stress, $F/2\pi RT_f$ |
| $T_f$ | Frontal wall thickness |
| $T_v$ | Vertical wall thickness |
| $W_o$ | Orifice width |
| $W_z$ | Zooid width |
| $Z_a$ | Number of zooids per probe area, $A_p/A_z$ |

## APPENDIX 2

*Puncture tests*

| Species | Region | Stress Mean ($MNm^{-2}$) | Stress S.D. ($MNm^{-2}$) | Shear stress Mean ($MNm^{-2}$) | Shear stress S.D. ($MNm^{-2}$) | Displacement Mean ($MNm^{-4}$) | Displacement S.D. ($MNm^{-4}$) | Sample size |
|---|---|---|---|---|---|---|---|---|
| *Drepanophora tuberculatum* | Edge | 83.95 | 56.84 | 22.15 | 14.99 | 0.89 | 0.31 | 8 |
| | Inner | 285.98 | 96.51 | 75.45 | 25.46 | 1.36 | 1.19 | 10 |
| | Ovicell | 94.59 | 29.95 | — | — | — | — | 7 |
| *Parellisina latirostris* | Edge | 0.81 | 0.43 | 2.59* | 1.38 | 0.94 | 0.21 | 10 |
| | Inner | 1.49 | 0.64 | 4.76 | 2.05 | 1.29 | 0.34 | 10 |
| | Ovicell | 52.82 | 45.35 | — | — | — | — | 2 |
| *Reptadeonella bipartita* | Edge | 126.77 | 54.03 | 44.46 | 18.95 | 0.63 | 0.62 | 10 |
| | Inner | 327.29 | 36.14 | 90.51 | 9.99 | 0.62 | 0.25 | 10 |
| | Operculum opening | 423.69 | 55.16 | — | — | — | — | 10 |
| *Reptadeonella costulata* | Edge | 67.72 | 33.27 | 15.71 | 7.71 | 1.81 | 0.67 | 12 |
| | Inner | 159.56 | 40.31 | 32.78 | 8.28 | 1.01 | — | 10 |
| *Steginoporella magnilabris* | Edge | 22.22 | 1.11 | 2.90 | 1.46 | 0.99 | 0.32 | 10 |
| | Inner | 7.05 | 2.52 | 7.51 | 2.68 | 1.16 | 0.32 | 10 |
| | Operculum hinge | 1.59 | 0.96 | — | — | — | — | 9 |
| *Steginoporella* sp. nov. A-zooids | | | | | | | | |
| | Edge | 4.99 | 1.39 | 6.52 | 1.82 | 3.11 | 0.47 | 11 |
| | Inner | 7.98 | 2.69 | 9.18 | 3.09 | 1.75 | 0.24 | 12 |
| | Operculum hinge | 4.56 | 1.31 | — | — | — | — | 11 |
| B-zooids | | | | | | | | |
| | Inner | 11.76 | 2.64 | 10.57 | 2.37 | 1.79 | 0.41 | 10 |
| | Operculum hinge | 6.04 | 1.96 | — | — | — | — | 10 |
| *Stylopoma spongites* | Edge | 33.67 | 18.24 | 17.61 | 9.54 | 0.63 | 0.35 | 10 |
| | Inner | 221.05 | 38.82 | 87.09 | 15.29 | 0.05 | 0.02 | 11 |
| | Operculum hinge | 2.49 | 1.41 | — | — | — | — | 11 |
| | Operculum opening | 111.98 | 32.86 | — | — | — | — | 11 |
| | Ovicell wall | 70.27 | 18.98 | — | — | — | — | 8 |
| *Trematooecia aviculifera* | Edge | 290.98 | 133.29 | 83.68 | 38.33 | 0.23 | — | 10 |
| | Inner | 457.37 | 114.39 | 89.48 | 22.38 | 0.06 | 0.05 | 11 |
| | Operculum hinge | 2.73 | 1.47 | — | — | — | — | 2 |
| | Operculum opening | 374.83 | 61.13 | — | — | — | — | 10 |
| | Ovicell membrane | | 5.65 | — | — | — | — | 8 |
| | Ovicell wall | 5.07 | 10.03 | — | — | — | — | 8 |
| | | 22.11 | | | | | | |

* Based on thickness of inner zooids.
Stress = F/A = Force/$\pi R^2$.
Shear stress = $F/2\pi RT_f$, $T_f$ is frontal wall thickness.

APPENDIX 3

*Compression tests*

| Species | Region | Stress = F/A Mean $(MNm^{-2})$ | Stress = F/A S.D. | Displacement Mean $(MNm^{-4})$ | Displacement S.D. | Force/Lateral Wall Area Mean | Sample Size |
|---|---|---|---|---|---|---|---|
| *Drepanophora tuberculatum* | Edge | 16.89 | 2.06 | 2.64 | 0.41 | 18.42 | 8 |
| | Inner | 27.17 | 6.05 | 2.24 | 0.59 | 33.80 | 10 |
| *Parasmittina* sp. | Inner | 15.81 | 5.28 | 1.42 | 0.44 | 45.03 | 7 |
| *Parellisina latirostris* | Inner | 6.54 | 3.98 | 0.83 | 0.19 | — | — |
| *Reptadeonella bipartita* | Edge | 12.57 | 3.58 | 1.12 | 0.27 | 8.22 | 4 |
| | Inner | 23.83 | 8.38 | 1.93 | 0.35 | 29.28 | 10 |
| *Reptadeonella costulata* | Edge | 14.29 | 9.18 | 3.03 | 1.10 | 17.95 | 13 |
| | Inner | 26.78 | 2.71 | 2.26 | 0.45 | 17.53 | 10 |
| *Steginoporella magnilabris* | A-zooids Inner | 11.33 | 2.48 | 1.42 | 0.52 | 71.17 | 10 |
| | B-zooids Inner | 14.66 | 4.24 | 1.93 | 0.64 | — | 10 |
| *Steginoporella* sp. nov. | Edge | 4.47 | 2.01 | 2.75 | 0.73 | 54.51 | 10 |
| | Inner | 14.90 | 2.43 | 3.52 | 0.90 | 110.13 | 10 |
| *Stylopoma spongites* | Edge | 6.27 | 3.36 | 0.61 | 0.11 | 17.12 | 10 |
| | Inner | 12.97 | 4.42 | 1.72 | 0.55 | 31.49 | 12 |
| *Trematooecia aviculifera* | Edge | 6.98 | 3.18 | 0.98 | 0.32 | 14.86 | 10 |
| | Inner | 13.35 | 3.58 | 0.87 | 0.35 | 22.90 | 11 |

## APPENDIX 4

*Morphometrics of encrusting bryozoans studied*

| Species: Region | Means (mm) | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Zooid | | | | Orifice | | | | Wall thickness | | | | Cavity depth | | | | Ovicell | | | | | |
| | Length | S.D. | Width | S.D. | Length | S.D. | Width | S.D. | Frontal | S.D. | Lateral | S.D. | Center | S.D. | Edge | S.D. | Length | S.D. | Width | S.D. | Height | S.D. |
| *Drepanophora tuberculatum* | | | | | | | | | | | | | | | | | | | | | | |
| Edge zooids | .382 | .025 | .286 | .026 | .102 | .026 | .086 | .008 | .109 | .017 | .037 | .007 | .111 | .024 | .066 | .014 | .116 | .012 | — | — | .137 | — |
| Inner zooids | .426 | .031 | .331 | .012 | .126 | .012 | .076 | .008 | | | | | | | | | | | | | | |
| *Parellisina latirostris* | | | | | | | | | | | | | | | | | | | | | | |
| Edge zooids | .424 | .055 | .400 | .028 | .064 | .006 | .144 | .012 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Inner zooids + OV | .506 | .023 | .391 | .050 | .089 | .004 | .154 | .021 | .009* | — | .008 | .003 | .116 | .024 | .086 | .018 | — | — | — | — | — | — |
| *Reptadeonella costulata* | | | | | | | | | | | | | | | | | | | | | | |
| Autozooids: | | | | | | | | | | | | | | | | | | | | | | |
| Edge | .732 | .086 | .437 | .049 | .109 | .006 | .151 | .091 | .124 | .020 | .054 | .009 | .224 | .028 | .164 | .035 | — | — | — | — | — | — |
| Inner | .819 | .013 | .457 | .056 | .127 | .009 | .155 | .011 | .140 | .053 | .112 | .028 | .224 | .008 | .149 | .015 | — | — | — | — | — | — |
| Gonozooids | .657 | .047 | .524 | .017 | .078 | .018 | .198 | .022 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Avicularian zooids | .846 | .032 | .622 | .032 | .133 | .019 | .127 | .016 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Reptadeonella bipartita* | | | | | | | | | | | | | | | | | | | | | | |
| Edge zooids | .496 | .033 | .337 | .019 | .060 | .005 | .096 | .010 | .082 | .026 | .038 | .009 | .148 | .011 | .168 | .109 | — | — | — | — | — | — |
| Inner zooids | .546 | .036 | .320 | .024 | .060 | .008 | .098 | .008 | .104 | .024 | .041 | .006 | .157 | | .100 | .029 | — | — | — | — | — | — |

| | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Trematooecia aviculifera* | | | | | | | | | | | | | | | | | | | | | | |
| Edge zooids | .815 | .092 | .586 | .046 | .174 | .008 | .207 | .018 | .100 | .038 | .040 | .007 | .285 | .020 | .173 | .024 | | | | | | |
| Inner zooids + ovicell | .837 | .069 | .677 | .084 | .193 | .021 | .222 | .015 | .147 | .018 | .054 | .013 | .333 | .060 | .202 | .052 | .395 | .044 | .477 | .070 | — | |
| Ovicell memb. window | | | | | | | | | | | | | | | | | .209 | .027 | .207 | .028 | — | |
| *Steginoporella* sp. nov. | | | | | | | | | | | | | | | | | | | | | | |
| A-Zooids: | | | | | | | | | | | | | | | | | | | | | | |
| Edge | 1.080 | .048 | .688 | .053 | .486 | .036 | .605 | .055 | .022 | .005 | .008 | .001 | .584 | .065 | .528 | .041 | — | — | — | — | — | — |
| Inner | 1.138 | .039 | .747 | .022 | .529 | .016 | .670 | .023 | .025 | .008 | .015 | .005 | .524 | .061 | .479 | .058 | — | — | — | — | — | — |
| B-Zooids | | | | | | | | | | | | | | | | | | | | | | |
| Edge | 1.890 | — | .972 | — | .810 | — | .900 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Inner | 1.933 | .149 | .936 | .065 | .954 | .074 | .911 | .084 | .032 | .006 | .013 | — | .514 | — | .469 | — | — | — | — | — | — | — |
| *Steginoporella magnilabris* | | | | | | | | | | | | | | | | | | | | | | |
| A-Zooids | | | | | | | | | | | | | | | | | | | | | | |
| Edge | .871 | .086 | .533 | .001 | .414 | .013 | .468 | .025 | .022 | .005 | .013 | .006 | .395 | .028 | .346 | .057 | — | — | — | — | — | — |
| Inner | .817 | .076 | .580 | .082 | .367 | .037 | .450 | .055 | .027 | .013 | .013 | .005 | .388 | .030 | .264 | .020 | — | — | — | — | — | — |
| B-Zooids | | | | | | | | | | | | | | | | | | | | | | |
| Edge | 1.184 | .047 | .644 | .060 | .583 | .027 | .594 | .051 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Inner | 1.116 | .055 | .587 | .050 | .500 | .030 | .536 | .069 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Stylopoma spongites* | | | | | | | | | | | | | | | | | | | | | | |
| Edge zooids | .610 | .076 | .382 | .052 | .122 | .017 | .120 | .014 | .055 | .009 | .021 | .002 | .164 | .055 | .106 | .052 | — | — | — | — | — | — |
| Inner zooid + ovicell | .602 | .020 | .422 | .023 | .146 | .009 | .120 | .010 | .073 | .009 | .025 | .060 | .211 | .012 | .147 | .025 | .586 | .012 | .497 | .020 | .182 | — |